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ABSTRACT

Capsule: Collective roosting behaviour of the Cattle Egret *Bubulcus ibis* was influenced by the weather and the season.

Aims: To document the roosting behaviour of the Cattle Egret and assess the relationship between weather conditions and four components of the roosting behaviour including the population size, duration of roost occupancy, the timing of roost gathering and the rate of arrival at roost.

Methods: We recorded the number and arrival times of individuals occupying a communal roost site in northeast Algeria in 2013–2014 between December and April.

Results: There was a seasonal decline of the flock size and rate of arrival and a seasonal increase in the duration of gathering. Weather conditions affected all variables assessed in roosting behaviour such that bad weather lowered the number of individuals in the roost, lengthened the duration and advanced the timing of gathering, and reduced the rate of gathering in the roost.

Conclusion: Our study highlights the importance of weather conditions in shaping the collective roosting behaviour of a gregarious species. Our results suggest that future changes in climatic conditions might influence the collective behaviour of the Cattle Egret in particular and gregarious birds in general.

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Many aspects of the ecology and behaviour of birds are affected by abiotic conditions (Newton 1998, Elkins 1983). Because physiology is influenced by weather and particularly temperature and rainfall (Moss *et al.* 2001, Crick 2004, Hallett *et al.* 2004), studies have reported intraspecific geographic variation of bird behaviour (Seghers 1974, Kroodsma *et al.* 1999), including collective behaviour (Rubenstein & Lovette 2007, Jetz & Rubenstein 2011). While large scale studies are useful for understanding the adaptation and plasticity of birds to the large-scale variation in environmental conditions (Jetz & Rubenstein 2011), there is has been little research on the fine-scale temporal variation of those conditions (governed by daily fluctuations of weather conditions) on the collective behaviour of birds. This area of research is timely given the expected increase of weather fluctuations in most future climate change scenarios (Intergovernmental Panel on Climate Change 2014).

Collective behaviour in birds is a central topic in ornithology in particular and in ethology in general (King & Sueur 2011, Biro *et al.* 2016, Maldonado-Chaparro *et al.* 2018). Two important aspects of collective behaviour are group coordination and decision-making (King & Sueur 2011) where individuals in groups with better coordination and decision-making outperform those with poor coordination and decision-making (Krause *et al.* 2002, Fernández-Juricic *et al.* 2004). Collective behaviour in foraging and migration contexts has attracted a lot of research attention (Bertram 1980, Lima 1995, Newton 2008), however, collective behaviour in the context of roosting (Evangelista *et al.* 2017) and particularly its relationship with weather conditions has not been as thoroughly studied. It is reasonable to assume that as with foraging sites, there is roost site selection in birds where individuals try to reach the roost early enough before sunset to guarantee a favourable position that

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shelter the birds from the weather (Robinson *et al.* 2007) and predation risk (Zahavi 1971, Hilton *et al.* 1999).

One of the most widespread gregarious birds in the world is the Cattle Egret *Bubulcus ibis* (Del Hoyo *et al.* 1992). This species has shown a rapid range shift towards northern areas during the last few decades (Maddock & Geering 1994), occupying natural habitats as well as rural and urban areas. This species shows a remarkably diverse diet and habitat use (terrestrial and aquatic) (Siegfried 1971b, Grubb 1976, Lombardini *et al.* 2001), which may underpin its ability to increase its population size. While the species forages in groups (Scott 1984), it frequently roosts in large flocks on tall trees near human settlements during the wintering season (Siegfried 1971a). The roosting behaviour of the species has received little research attention, although it represents an interesting system to ask behavioural and evolutionary questions (Zahavi 1971, Evangelista *et al.* 2017). Here, we investigate how weather affects the roosting timing of Cattle Egrets in northeast Algeria in the winter and spring. Specifically, we assess the duration and timing of arrival of individuals to the roosting site, the roosting population size and the synchronization of roost arrival.

The weather affects many cues used by birds for decision making (Richardson 1978, Elkins 1983), and thus it shapes the time allocated for foraging, the distribution of individuals and possibly the timing of roosting. In this study, we hypothesize that weather does not change the number of individuals in the roosting site, but influences the rate and the timing of arrivals such that better weather leads to more synchronized arrival to the roosting site (Figure 1). Additionally, bad weather might induce individuals to roost earlier because food availability is lower. It is also possible that the rate of gathering is higher in bad weather because individuals might need to compete more to occupy sheltered area.

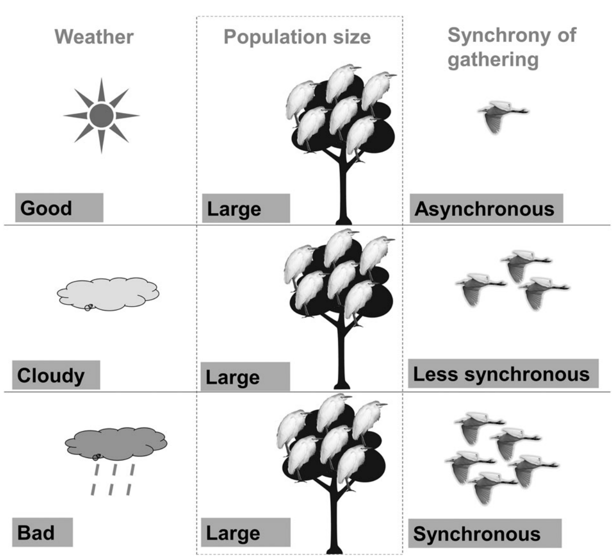

Figure 1. Potential effects of weather conditions on the population size at roost sites and synchrony of gathering during roosting of the Cattle Egret. We hypothesize that weather conditions should not change the population size at roosting sites, but could affect the timing and synchrony of arrivals. The prediction is that arrivals should be more synchronous in bad weather than in good weather.

Methods

Study area

The study was conducted in Berrihane, El Taref, Algeria, 4 km south of the Mediterranean Sea. The roosting site was near the national road W109 in the northeast of the Mekhada marsh (36.8426°N, 8.0623°E), an 8900 ha wetland listed as an Important Bird Area (IBA) and ranked as the second-largest wetland in the country. This wetland is known for harboring large numbers of wintering waterbirds (about 30,000 birds), including the Marbled Duck *Marmaronetta angustirostris* and breeding waterbirds such as the Ferruginous Duck *Aythya nyroca* and the White-headed Duck (*Oxyura leucocephala*) (BirdLife International 2019).

The Cattle Egret population has shown a rapid expansion in Algeria, where it winters and breeds extensively (Si Bachir *et al.* 2000, 2011). The studied roosting site of the Cattle Egret occurred in a patch of tall (10–40 m high) Tasmanian Blue Gum trees *Eucalyptus globulus* which occupied an area of 0.4 ha. Only 3–4 trees were used as roosts by the Cattle Egret and thus were surveyed. Despite the availability of other nearby patches of trees (100 m way) which could potentially be used as roosts, no other roosting sites were recorded in the proximity. No other species of bird occupied the communal roost during the study.

Behavioural sampling

We recorded the number of individuals and the timing of gathering in the roosting site from 16:00 to 20:00 between 24 December 2013 and 20 April 2014 on 22 sampling occasions. We observed the roost from a distance of about 40 m from the trees. The number of individuals was usually easy to estimate by eye since the Cattle Egret arrived in groups. We also recorded the time at which the groups arrived, thus we were able to estimate the time of the first and last arrival and the duration of gathering in the roost site (time of the last arrival – time of the first arrival). The latter is a relative measure of coordination of the roosting behaviour in the Cattle Egret. By dividing the number of Cattle Egrets recorded in each sampling occasion by the duration of arrivals (occupancy of the roost), we calculated the rate at which individuals gathered in the roosting site. Because weather might affect the roosting collective behaviour of Cattle Egrets, we recorded the weather on each sampling occasion. The weather was classified into three categories: (1) good weather when the sky was clear, no significant clouds and no wind, (2) cloudy weather when the sky was mostly cloudy with light rain and/or moderate winds and (3) bad weather when it was raining, the sky was cloudy (almost fully covered), and/or strong winds.

Statistical analysis

All statistical analyses were conducted in R 3.3.2 (R Development Core Team 2019). The effects of the season (continuous variable) and weather (categorical variable) were tested on population size at the roosting site, duration of the arrivals, time of the first arrival, time of the last arrival, and the rate of arrival of individuals with analysis of variance (ANOVA), including the two main effects and their interaction. The package *chron* was used to use time data as a continuous response variable (James & Hornik 2018). The relationship between population size and gathering duration was tested using Spearman's correlation test. Reported values are mean ± sd.

Results

Roosting population size

The roosting population size varied between 552 and 3744 during the study period, showing a mean of 2324 ± 811.5. There was a clear decline of the population size from December to April (Figure 2), revealed by the significant negative effect of the season (ANOVA: $F_{1,16} = 16.0$, $P = 0.001$). The non-significant interaction between weather and season (ANOVA: $F_{2,16} = 0.23$, $P = 0.79$) shows that this population decline at the roosting site occurred similarly irrespective of the weather conditions. Importantly, the significant weather effect shows that population size varied with weather conditions (ANOVA: $F_{2,16} = 7.6$, $P = 0.004$). The mean population size was 2748 ± 541, 2234 ± 885, and 1603 ± 541 in good, cloudy and bad weather, respectively.

Roosting timing and arrival duration

The analysis of the roosting timing was conducted based on the duration of gathering and the time of the first and

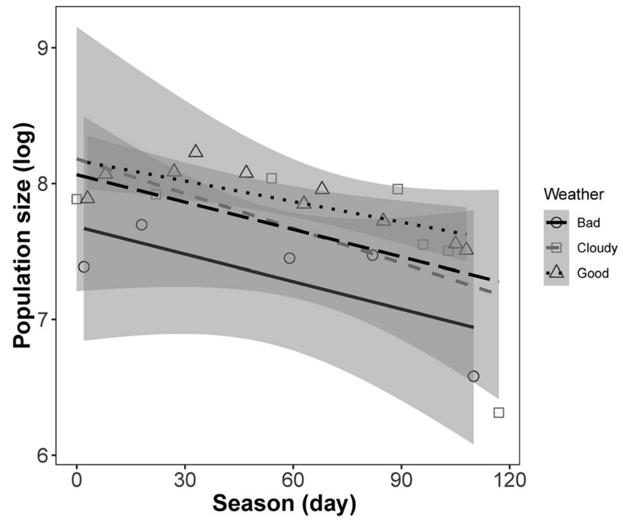

Figure 2. The seasonal pattern of population size (with logarithmic transformation) in the Cattle Egret roost in different weather conditions. The regression lines are simple linear and the grey ribbons are standard errors. The black dashed line is the average regression across all weather conditions. Day 0 is December 24th and the last day of sampling is April 4th.

last arrival of the roosting Cattle Egrets. For the duration of the gathering, the significant positive effect of the season (ANOVA: $F_{1,16} = 9.79$, $P = 0.006$) shows that the duration of arrivals at the roosting site increased across the wintering season (Figure 3). On average, it took 68.2 ± 20.86 min ($N = 22$) for the entire population to occupy the roost site, and the duration increased by 0.22 min per day ($R^2 = 0.18$, $P = 0.04$) throughout the study period. The non-significant interaction between

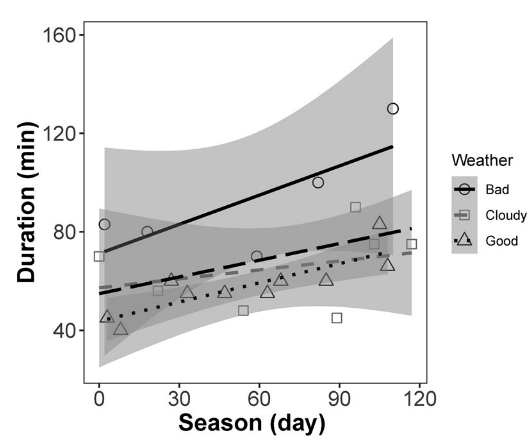

Figure 3. The seasonal pattern of the duration of gathering at the Cattle Egret roost in different weather conditions. The regression lines are simple linear and the grey ribbons are standard errors. The black dashed line is the average regression across all weather conditions. Time on B and C is linearized. Day 0 is December 24th and the last day of sampling is April 4th.

season and weather (ANOVA: $F_{2,16} = 1.04$, $P = 0.37$) shows that the pattern of the seasonal increase was similar among weather conditions. The significant weather effect shows that there was a condition-dependent gathering duration (ANOVA: $F_{2,16} = 12.3$, $P = 0.0005$). In bad weather, the duration of arrivals was longer than in cloudy and good weather. In addition, there was a negative correlation between population size and gathering duration (Spearman's correlation: $r = -0.78$, $P < 0.0001$).

For the timing of arrivals, there was a positive effect of the season on time of first (ANOVA: $F_{1,16} = 43.8$, $P < 0.0001$) and last arrival (ANOVA: $F_{1,16} = 96.9$, $P < 0.0001$), showing that the first and last groups arriving at the roost became progressively later towards the end of the wintering season (Figures 4 and 5). On average, Cattle Egrets started to occupy the roost at 17:05 h and finished at 18:13 h (local time). However, the interaction between the season and weather was not significant in the time of the first and last arrival (ANOVA: $F_{2,16} = 1.47$, $P = 0.25$). The seasonal effect was significant in the time of the first arrival (ANOVA: $F_{2,16} = 18.1$, $P < 0.0001$) but not of the last arrival at roosting sites (ANOVA: $F_{2,16} = 3.25$, $P = 0.06$). In fact, the first individuals to occupy the roost returned earlier in bad weather (Figure 4).

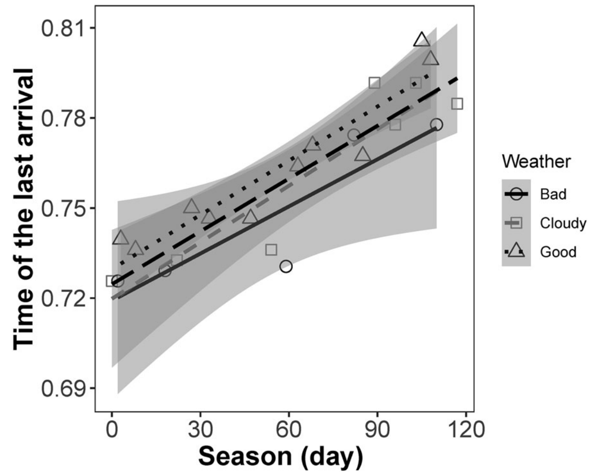

Figure 5. The seasonal pattern of the time of the last arrival to the Cattle Egret roost in different weather conditions. The regression lines are simple linear and the grey ribbons are standard errors. The black dashed line is the average regression across all weather conditions. Time is linearized. Day 0 is December 24th and the last day of sampling is April 4th.

Rate of arrival at the roosting site

The rate of arrival at the roosting site was calculated as the number of individuals arriving divided by the time between the first and last arrival (Figure 6). The mean rate of arrival at the roost was 39.3 ± 21.0 birds per minute ($N = 22$). There was a seasonal decline in the rate of the arrival of individuals to the roost (ANOVA: $F_{1,16} = 14.8$, $P = 0.001$). There was no significant effect of the interaction between weather and season (ANOVA: $F_{2,16} = 1.29$, $P = 0.30$), showing that the seasonal pattern of the rate of arrival of individuals was similar in different weather conditions. The weather effect shows that the rate of arrival of individuals was

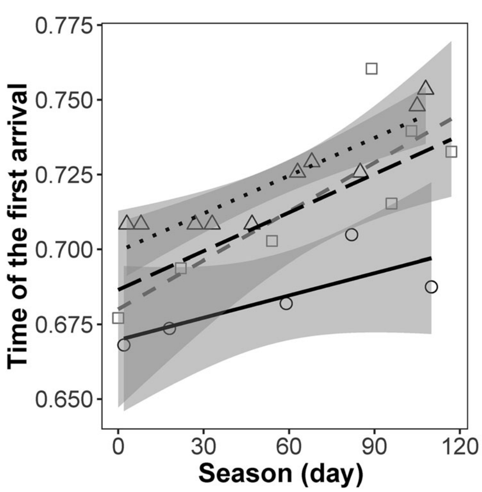

Figure 4. The seasonal pattern of the time of the first arrival at the Cattle Egret roost in different weather conditions. The regression lines are simple linear and the grey ribbons are standard errors. The black dashed line is the average regression across all weather conditions. Time is linearized. Day 0 is December 24th and the last day of sampling is April 4th.

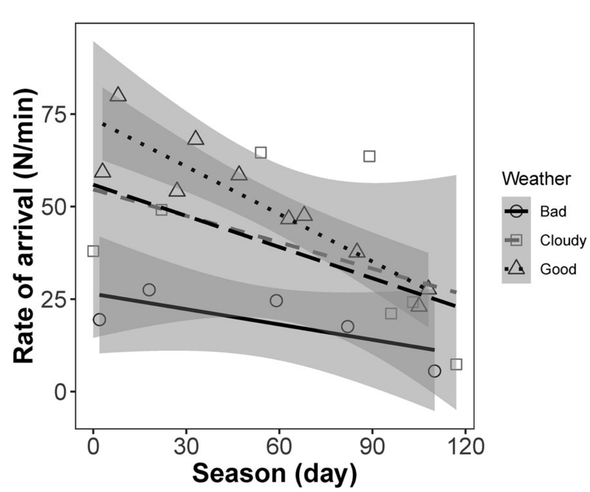

Figure 6. The seasonal pattern of the rate of arrival of individual Cattle Egrets to the roosting site in different weather conditions. The regression lines are simple linear and the grey ribbons are standard errors. The black dashed line is the average regression across all weather conditions. Day 0 is December 24th and the last day of sampling is April 4th.

greater in good and moderate weather than in bad weather conditions (ANOVA: $F_{2,16} = 9.37$, $P = 0.002$).

Discussion

Our study shows that there was seasonal variation in the collective roosting behaviour of Cattle Egrets and that weather influenced the number of individuals, the duration and timing of arrivals, and the rate of arrival at the roosting site. More specifically, in good weather, the number of individuals was larger, the duration of arrivals was shorter, the timing was delayed, and the rate of arrival was faster. Interestingly, we showed that the effect of season (time of the year) was almost as strong as that of the weather. The understanding of the mechanisms mediating those climate-dependent roosting behaviours will help us predict how future changes in climatic conditions will influence the collective behaviours of gregarious birds.

The number of individuals in the roost site was highly dependent on the season where higher numbers were observed in the winter and lowest numbers in the spring. This seasonal pattern is consistent with the natural history of the species. In March and April, when the Cattle Egret breeding season starts, the species leaves the wintering roosting sites and occupies breeding sites. The species is known to start building nests during April (Bachir *et al.* 2008, Sbiki *et al.* 2015), which is consistent with the declining pattern of the roosting population size. Interestingly, different from our expectation (Figure 1), weather conditions heavily influenced the number of individuals in the roost during the wintering season. Larger numbers were recorded in good and cloudy weather, but significantly lower numbers were recorded in bad (rainy) weather. While bad weather conditions are known to reduce the number of birds in the wild (Robbins 1981), observing a similar pattern in roosts is curious and it suggests that the roosting group splits into different roosts. Similar roosting behavioural patterns were observed in European Starlings *Sturnus vulgaris* during bad weather (Elkins 1983). There are two mutually non-exclusive hypotheses to explain the cohort splitting. First, birds might tend to find the nearest shelter available during bad weather to avoid getting wet or reduce predation risk (due to lower predator detectability). Second, cohort splitting might be related to the limited availability of sheltered positions within a single roost. Nye (1964) showed that if an individual bird is in good condition (healthy and has large internal reserves), getting wet induces it to lose a lot of energy while maintaining its body temperature, but if the individual is in poor condition, wetting might lead to severe heat loss, hypothermia and ultimately death. Further studies based on marked individuals will reveal the population structure and the distance travelled by the sub-groups to find new roosts.

The synchronization of arrival at roosts decreased (increase in the duration of arrival) across the wintering season. This asynchronization was the result of the last arriving birds arriving disproportionately later to the roosts. This change in the timing of arrivals at roosts is probably partly due to the seasonal increase in the length of the day. In longer days, individuals probably stayed longer at foraging sites and used sunset as a cue to time roosting (Lucia & Osborne 1983). However, the weather conditions affected the duration of the arrivals. In bad weather, the timing of the first arrival was earlier and that of the last arrival remained relatively unaffected, resulting in an increase in the duration of the arrivals. There are three mutually non-exclusive hypotheses to explain this behavioural pattern. First (the predation hypothesis), the Cattle Egrets could have returned to the roost earlier on rainy days because of predation risk. There could be an interaction between predation risk and weather conditions such that predation risk was greater in bad weather conditions. Hilton *et al.* (1999) suggest that precipitation may increase predation risk of Common Redshanks *Tringa totanus* by European Sparrowhawks *Accipiter nisus* due to lower detection capacity by the prey species. Thus, it is possible that the Cattle Egrets occupied roosts earlier in bad weather conditions to avoid predation. Second (the competition hypothesis), we hypothesize that bad weather induces intraspecific competition for more sheltered sites (scramble competition for sheltered roost microhabitats; Kennedy 1970). It is reasonable to assume that the carrying capacity of sheltered locations in the roost is smaller than that of the total number of locations (including sheltered and unsheltered locations). Thus, early arrival allows individuals to select the best or most appropriate sites within the roost. Third (the orientation hypothesis), given the wealth of literature showing that bad weather influences the orientation of flight in many birds (Richardson 1978, Elkins 1983), we hypothesize that inclement weather alters the group coordination and leads to splitting into different independent sub-units which make different decisions with respect to roost timing (self-organization; Couzin & Krause 2003).

The rate of arrival at the roosting site declined with the season and was dependent on the weather conditions. The seasonal decline in the rate of arrival was the results of the seasonal decline of the number of individuals and the increase of the duration between the first and last arrival of birds in the roost. Contrary to our prediction, the rate of arrival was faster in good weather and slower in bad weather. This shows seasonal and weather-dependent group coordination in roosting behaviour. Although the ecological seasonality effects on group coordination have been investigated in primates (Doran 1997, Scholz & Kappeler 2004, Pyritz *et al.* 2011), it has received less attention in birds for non-migratory and non-dispersive movements (Walls *et al.* 2005). It is still too premature to speculate on the factors and behavioural mechanisms that control decision making and group organization, this is why further investigation in this area is needed to shed light on group behaviour.

This study is probably the first to assess the collective behaviour and timing of roosting behaviour in Cattle Egrets; an aspect that has received little attention in Ardeidae and other gregarious groups. Our results reveal that weather conditions have a major effect on the size of the roosting flock, the duration and timing of roosting and the rate of arrival at the roost. These findings suggest that the spatial distribution and the behavioural decisions of gregarious species might be heavily influenced by climate change in the future which is expected to affect the frequency, distribution and intensity of rainfall (Prein *et al.* 2017, Zhang *et al.* 2017, Schroeer & Kirchengast 2018). Thus, a clear understanding of these mechanistic eco-physiological dynamics is a priority in global change avian research. The next step is to follow tagged individuals (preferably telemetry tagging) to pinpoint the factors that drive group coordination and decision making in the light of the existing landscape. While this study was conducted on a single site, we recommend future studies to investigate different roosting sites simultaneously to understand whether climatic conditions induce individuals to split into different nearby or farther sites. Finally, our results may apply to other gregarious birds that forage and roost in flocks.

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